

MOLT AND BODY MASS OF RED KNOTS IN THE EASTERN UNITED STATES

BRIAN A. HARRINGTON,^{1,3} BRADFORD WINN,² AND STEPHEN C. BROWN¹

ABSTRACT.—Red Knots (*Calidris canutus*) that spend winter in the southeastern United States are known to have been genetically separated from their congeners that migrate to Patagonian wintering grounds for about 12,000 years. We examined and documented differences between the two groups in their use of southward migration stopover locations, flight feather molt, fidelity to wintering zones, and differences in mass at southward migration stopover locations. Red Knots wintering in the southeastern United States do so consistently, and knots wintering in Patagonia have not changed to wintering in the southeastern United States. The two wintering groups have distinct differences in their nonbreeding season biology (e.g., migration strategies, chronology of pre-basic molt), and these differences have been maintained for decades if not millennia. Received 24 August 2004. Accepted 22 July 2006.

Red Knots (*Calidris canutus*), a Holarctic breeding shorebird, have a relatively large, albeit poorly-known breeding range in the Nearctic (Harrington 2001). There are at least two regions in the Western Hemisphere where relatively large numbers of Red Knots are known to spend their winter, one on the Patagonian coasts of Argentina and Chile (Patagonian-wintering knots), and the other (northern-wintering knots) ~9,500 km to the north, including areas in the southeastern United States (Morrison and Harrington 1992). Based on evidence of differing migration strategies and differential survival estimates for these two wintering groups, Harrington et al. (1988) questioned whether knots from the Patagonian and U.S. wintering regions were from different breeding groups with little genetic exchange. Buehler and Baker (2005) confirmed that Patagonian-wintering and northern-wintering knots have been genetically isolated for about 12,000 years. Little additional information is known about how these two groups differ in their biology.

The objectives of our study were to explore the possibility that Red Knots wintering in the U.S. differed from those wintering in Patagonia in flight-feather molt, movement of color-banded birds, plumages, and migration chronology. We tested the hypotheses that Patagonian and northern-wintering knots have

developed distinctly different migrations as reflected in differences of their flight-feather molt, migration-related mass gain, principal migration stopover locations, as well as wintering locations.

METHODS

Study Areas.—We studied two regions used by knots during southward migration: Cape Cod and western Cape Cod Bay in Massachusetts, and the Altamaha River Estuary on the Georgia Atlantic coast. Sites in Massachusetts included Third Cliff Beach (42° 10' N, 70° 43' W), and Monomoy Island and South Beach in Chatham (41° 38' N, 69° 58' W). In Georgia we worked mostly on Wolf Island (31° 19' N, 81° 17' W), Little Egg Island Bar (31° 18' N, 81° 16' W), and Little St. Simons Island (31° 17' N, 81° 16' W). Additional observations were on the Florida west coast, principally between Bonita Springs (26° 24' N, 81° 54' W) and Honeymoon Island in Dunedin (28° 04' N, 82° 50' W).

Capture and Banding.—We captured knots using rocket and cannon nets placed at locations where flocks of knots gathered at high-tide roosts during the day. We used trained, volunteer crews to remove captured birds from nets to well-ventilated holding containers prior to processing. Standard, uniquely-numbered U.S. Federal bands and color bands were applied to tarsi and meta-tarsi in combinations to allow visual identifications of capture location and date. Birds were released at capture locations.

We used a rocket net in Massachusetts for capturing 1,363 adult Red Knots at Third Cliff

¹ Manomet Center for Conservation Sciences, P. O. Box 1770, Manomet, MA 02345, USA.

² Georgia Department of Natural Resources, One Conservation Way, Brunswick, GA 31523, USA.

³ Corresponding author;
e-mail: bharrington@manomet.org

Beach and Plymouth Beach (42° 59' N, 70° 39' W) during July and August, 1980–1983. Birds were evaluated for flight feather molt, and body mass to the nearest gram. Birds were processed and released on site. We assigned age (adult or juvenile) based on plumage characters (Hayman et al. 1986). During August 2004 and 2005 we also collected information on flight feather molt by watching flocks through telescopes when wing-stretching is commonly seen, i.e., shortly before flocks depart high-tide roosts for foraging areas (BAH, pers. obs.), and by careful scrutiny of close-by knots in flight.

We used a rocket net to capture, color-mark, and release knots during January ($n = 272$ adults) and October ($n = 99$ adults) 1981 at Longboat Key (27° 20' N, 82° 36' W) on the west coast of Florida. Birds from all catches were evaluated for flight feather molt, and were weighed to the nearest 0.1 g using a triple-beam balance. Birds were processed and released on site. We did not use data from individuals less than 12 months of age, based on plumage characters (Hayman et al. 1986).

We captured 226 adult knots in Georgia using a cannon net set at three high-tide roosting locations in the Altamaha River Estuary (31° 18' N, 81° 17' W). We processed most catches at the capture location, taking measurements of mass to the nearest 1.0 g using a Pesola[™] spring scale, and scoring the primary feather molt condition.

Migration Counts.—We used International Shorebird Survey (ISS) data collected between 1975 and 2004 to evaluate numbers of knots counted in the eastern United States between June and December. ISS project guidelines ask cooperators to count shorebirds at sites they choose three times a month during spring and autumn migration periods. Data evaluated for this study were those collected between 1 July and 31 December at sites on the Massachusetts coast (67 sites; 4,066 counts), the Georgia and South Carolina coast (16 sites; 415 counts), and the Florida coast (61 sites; 1,614 counts).

We began field study of knots in the Altamaha Estuary in Georgia in September 1998, and estimated numbers each year during September through 2003. We made no effort to estimate numbers systematically on regular

schedules at other times of year, but collected counts as opportunity allowed.

Primary Feather Molt.—Knots have a sequential primary flight-feather molt starting with the innermost feather and moving centrifugally (Ginn and Melville 1983). This enables scoring molt stages using the Ashmole (1962) system where each of the 10 primary feathers on the right wing can score between 0 and 5 points, depending on age and growth stage. A knot with 10 new primary feathers would score 50, one where the molt had progressed about half way from inner to outer primary feathers would score ~25, and one with 10 old primary feathers would score 0. Old primary feathers are distinguishable from new feathers by fading and extensive wear whereas new feathers are darker (less faded) with little wear. We scored the molt on samples of knots captured in Massachusetts, Georgia, and Florida. We used one-way ANOVAs to compare score means between years within study sites, and among study sites.

Color-band Searches.—We searched through flocks of knots in Massachusetts, Georgia, and Florida to find color-marked individuals, recording whether they were those we marked in Georgia, or ones marked by other researchers in Delaware Bay or South America. We used Chi-square analysis to compare the relative frequencies with which we found knots from these three banding origins.

Body Plumage Evaluation.—We recorded body plumage appearance of adult knots in Georgia, assigning scores ranging between 1 (complete basic plumage) and 5 (complete alternate plumage). These data were from knots randomly selected ($n = 143$) from flocks during studies of foraging birds on tidal flats close to our capture locations. Our samples in Massachusetts ($n = 346$) and Florida ($n = 225$) were from photographs of flocks taken at our capture locations. The plumages were scored as between 1 and 3 or between 4 and 5 because only partial views were possible from photographs. Results of statistical evaluations were considered significant at $P \leq 0.05$.

RESULTS

Autumn Migration Counts.—Peak counts of southward passage Red Knots in Massachu-

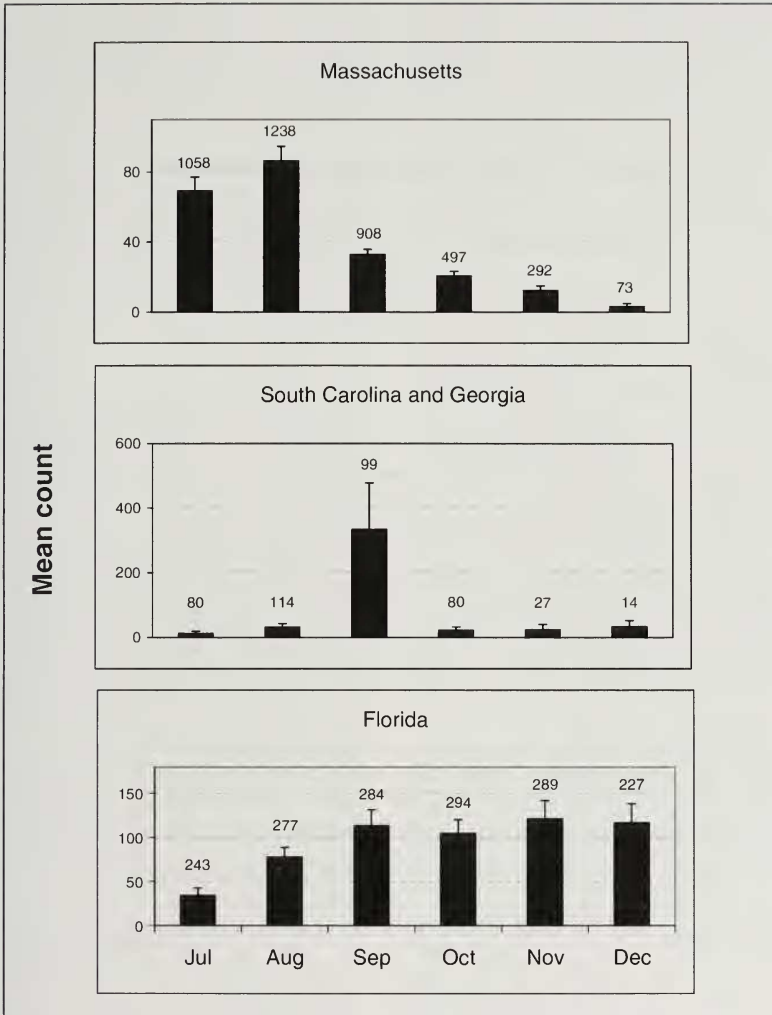


FIG. 1. Mean numbers (± 1 SE) of Red Knots counted between July and December by the International Shorebird Surveys (ISS).

sets were during the first third of August, well before peak numbers were counted on the South Carolina-Georgia and Florida coasts (Fig. 1). We did not document the full seasonal chronology of the knot passage in Georgia because we were present only during September. However, by canvassing a number of visitors and occasional visits by BW and BAH, we believe the general pattern was that numbers increased during August, reached peak abundance during late September, and declined during October (Fig. 1). Our separate counts at the Altamaha Estuary during September indicated that numbers of knots varied

considerably between years with maxima ranging from 5,000 (1999) to 10,000 (2001) birds.

Sightings of Color-banded Birds.—The information on the numbers of knots on the Massachusetts and Georgia coasts does not identify whether the knots visiting the Massachusetts coast were also visiting the Georgia coast. We believe that most knots transiting through Massachusetts during southward migration have South American destinations, and that most of those transiting through the Georgia stopover are enroute to U.S. or other northern wintering areas. We used resightings

TABLE 1. Numbers of Massachusetts and Georgia sightings during southward migrations (2003–2004) of Red Knots color-banded in either Georgia or South America.

Resighted in	Banded in	
	Georgia	South America
Georgia	82	9
Massachusetts	5	77
Florida	60	0

of color-banded knots at both locations in 2003 and 2004 to examine use of the Massachusetts and Georgia stopover locations in two ways: (1) the relative resighting frequencies of knots marked in Georgia and seen in Massachusetts, and (2) the relative resighting frequencies of Red Knots marked in South America and seen in Massachusetts as compared to Georgia. This comparison (Table 1) shows that substantially higher proportions of the knots transiting through Massachusetts versus Georgia have South American destinations.

We also compared the relative frequencies with which knots marked in either Georgia or South America were seen during winter (Nov–Feb 2003–2004) on the west coast of Florida, i.e., within the range of the northern

wintering group. These results (Table 1) show that many of the knots transiting the Georgia migration stopover area during September have winter-ground destinations on the Florida west coast. The results also indicate that some unknown, but small, fraction of knots transiting the Georgia stopover have South American winter-ground destinations. This was confirmed by sighting a small number of the thousands that had been color-banded in Patagonia.

Plumage.—During July and early August in Massachusetts, virtually all of the 346 adult knots whose plumage molt we scored from photographs had mostly alternate body plumage (scores between 4 and 5, $n = 332$). Few had actively molting body plumage feathers, and it appeared the pre-basic molt had begun but became arrested north of (or possibly in) Massachusetts. The few (i.e., low hundreds) of adult Red Knots remaining in Massachusetts between late August and October had progressively greater amounts of basic plumage, and were in virtually complete basic plumage by October.

Most of the adult knots at the Altamaha Estuary, Georgia were in predominately basic plumage by early September (Fig. 2), and more than half had attained virtually complete

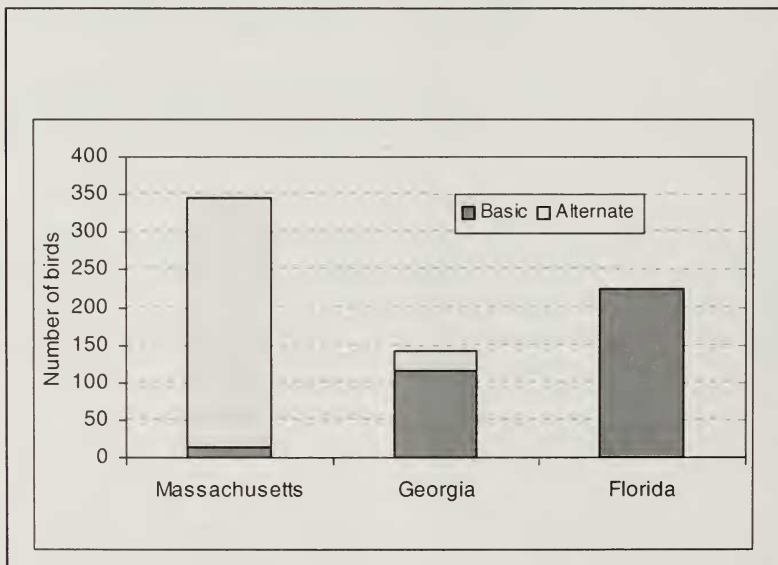


FIG. 2. Plumages (mostly alternate or mostly basic) of adult Red Knots in Massachusetts (Jul–early Aug), Georgia (Sep), and Florida (Oct).

basic plumage (i.e., the pre-basic molt was substantially more advanced than in Massachusetts). In Florida, during both October and January, virtually all adult knots were in basic plumage.

Primary Feather Molt.—We checked the primary flight feather molt in 1,363 adult knots captured on western Cape Cod Bay, Massachusetts during July and August, 1980–1983; all but two were prior to 13 August, after which date numbers of knots declined rapidly. We found no flight-feather molt among these knots.

In contrast to the above, BAH and Jake Walker found primary feather molt in 99 of 610 adult knots they checked on eastern Cape Cod during 2004 and 2005. Many of these birds appeared to be in a first basic plumage (dorsal body feathers substantially faded, with primary feather tips faded and heavily worn). In contrast, only one of 80 knots ($\chi^2 = 10.95$, $P < 0.001$) checked on western Cape Cod Bay (where banding occurred 1980–1983) showed primary feather molt.

We had sufficient captures in Georgia during September 2000–2002 to evaluate stages of primary feather molt in adult knots. We found no differences (ANOVA, $F_{2,194} = 0.72$, $P = 0.49$) of mean scores between years among knots actively or recently having completed (score 50) molt, and combined years for analysis. The average primary molt score of knots with actively growing feathers was 34.8 ($n = 171$, including 7 that were not weighed), indicating the typical molt had progressed from primary number 1 to primaries 6–8. There were some individuals ($n = 5$) with scores below 20 (involving primaries 1–4). In addition, others had recently completed the primary feather molt (score = 50, $n = 19$), and a few had 10 old primary feathers (score = 0, $n = 7$).

All but one of the 272 knots we captured in January 1981 in Florida had all new and fully grown primary flight feathers. Most knots (90 of 99 adults) on 10 October 1981 had growing primaries: the average score among 90 adults that were molting was 40.2 ± 0.53 . We compared this October value to the mean value of a single group of 72 (score mean = 34.7 ± 0.8 SE) captured at Altamaha Estuary, Georgia on 11 September 2001 (restricted to adults having active primary feather

TABLE 2. Body mass of adult Red Knots at different stages of primary feather molt during September 2000–2003 on the Georgia coast.

Groups	<i>n</i>	Mean weight (g)	SD
Primary score 0	7	141.0 ^a	12.0
Scores 7–49	169	132.1	10.4
Scores 50	19	149.6	22.6

^a Lower than the Massachusetts mean of 161.7 g in July/August.

molt). The Florida mean molt score from October was higher (ANOVA, $F_{1,160} = 22.2$, $P < 0.01$) than the mean score from mid-September in Georgia.

Body Mass.—The average mass of captured knots ($\bar{x} = 161.06 \pm 0.64$ SE, $n = 1,341$) in Massachusetts during July–August (1980–1983) was greater (ANOVA, $P < 0.01$) than for knots captured after August in Georgia ($\bar{x} = 134.4 \pm 0.9$, $n = 199$) or Florida during October ($\bar{x} = 124.9 \pm 0.7$, $n = 99$) and January 1981 ($\bar{x} = 137.1 \pm 0.7$, $n = 145$). Mean body mass of birds caught in Massachusetts on different dates generally increased until principal migration departures on ~10 August. For example, mean values were 132.3 ± 1.2 SE ($n = 161$) on 26 July 1983, 153.0 ± 1.2 on 1 August 1984 ($n = 146$), and 185.1 ± 1.3 ($n = 132$) on 7 August 1980.

Body mass of Red Knots in Georgia was lower (ANOVA, $F_{2,196} = 5.59$, $P = 0.004$) in 2001 versus 2000 or 2002. The knots during 2001 were foraging principally on sodbanks after their favored local prey (bivalves in the genera *Mulinex* and *Donax*) had largely disappeared. Weights of knots from Georgia were slightly more variable than at the Massachusetts and Florida sites. The annual variation of mass in Georgia was apparently related to annual differences in food resources.

We combined data from all years to compare the mean body mass of knots that were not molting primary flight feathers to those that were molting. Those molting were lighter (ANOVA, $F_{2,194} = 34.8$, $P < 0.001$) than knots that were not molting (Table 2).

DISCUSSION

We conclude from our data (Table 3) that Red Knots in Massachusetts and Georgia represent groups with distinctly different wintering destinations. Most that passage south

TABLE 3. Chronology and molt of Red Knots migrating south through Massachusetts and Georgia.

	Massachusetts	Georgia/Florida
Chronology	Depart mid-Aug	Depart in Oct
Principal months for primary feather molt	Nov–Jan in Patagonia	Aug–Nov in Georgia and Florida
Weight change	Rapid body mass gain in Jul/Aug	Little or slow mass gain in Sep
Body plumage molt	Alternate plumage in Aug, with arrested pre-basic molt	Little alternate plumage remaining in Aug, ongoing pre-basic molt
Color-banded birds from South America	Many with bands from South American wintering areas	Few with bands from South American wintering areas
Color-banded birds from Georgia	Few with bands applied during Sep in Georgia	Many in Florida banded during Sep in Georgia

through Massachusetts migrate to Patagonia, whereas most of those in Georgia winter in the Northern Hemisphere including the southeastern U.S. These results support earlier speculation (Harrington et al. 1988) and recent genetic studies (Buehler and Baker 2005) which show the two wintering areas are populated by separate groups of knots.

Counts During Autumn and Winter.—Numbers of southward migrating Red Knots increase on the Massachusetts coast during the second half of July and decline after reaching peak levels in the first or second third of August. The decline in Massachusetts (mid-Aug) occurs at about the same time that knots begin to appear in northern South America (Spaans 1978).

Our information from color banding as well as previous information (Harrington et al. 1988) shows that most knots on the Massachusetts coast during early August travel by direct, over-ocean flights to South America (Harrington 2001). It is possible that some knots departing Massachusetts follow the U.S. Atlantic coast southwards, comprising a small fraction of the knots that visit southeastern states.

The increase in numbers of knots in the southeastern U.S. begins in late July/early August as in Massachusetts. However, numbers in Georgia do not decline in August, but remain stable or perhaps continue to increase slowly between August and October, after the early October arrival dates of knots in Argentina (Harrington 2001). Knots marked in Georgia are commonly found on the Florida west coast, a contrast to their numbers found in Massachusetts (Table 1).

Plumage and Primary Feather Molt.—Red

Knots passing through Massachusetts during July and August have a predominately alternate plumage. Active pre-basic molt of body plumage in Massachusetts becomes arrested, and molt does not resume prior to the principal migration departure during mid-August (Morrison and Harrington 1992). The small numbers of adults that remain in Massachusetts after mid-August possibly represents birds that are enroute to southeastern U.S. states.

Most Red Knots in Georgia during August/September have ongoing pre-basic molt as evidenced by plumages changing from largely alternate to largely basic (Fig. 2). Most adult knots in Georgia also have active primary feather molt (Table 2), with the majority having molted slightly more than half of the primary feathers by mid-September.

Body Mass.—The average body mass for Red Knots in Georgia was greater in birds that were not molting flight feathers than in birds that were molting flight feathers. We interpret these data as evidence they were preparing for a long-distance, non-stop migration flight (Gudmundsson et al. 1991). An alternative idea is that non-molting knots were heavier simply because they were not molting, i.e., as a consequence of a presumed close relationship between active primary feather molt and low body mass (Lindström et al. 1994). However, Holmgren et al. (1993) found no relationship between body mass and presence or absence of flight feather molt in Dunlin (*Calidris alpina*).

It is generally believed that shorebirds do not gain mass unless preparing for migration (Burns and Ydenberg 2002) or for cold winter weather (Dugan et al. 1981). The mean mass

of 597 Red Knots wintering in Tierra del Fuego, Argentina during February, when primary feather molt was presumably completed, was 126.8 g (Baker et al. 1996). This average is ~14 g less than the average mass in the small sample of knots having molt scores of 0 in Georgia, and ~22 g less than the average for the Georgia knots that had all new primary feathers. Thus, there is insufficient evidence to show that knots without active primary feather molt would necessarily weigh more than knots that do have active primary feather molt.

CONSERVATION IMPLICATIONS

Our results confirm there are at least two distinct wintering groups of Red Knots in the Western Hemisphere. However, we do not know the relative proportions that historically used Delaware Bay during spring. The Patagonian wintering group, once estimated to be 100,000–150,000 knots (Morrison and Harrington 1992), is undergoing an alarming population decline, and now number fewer than 20,000 birds (Morrison et al. 2004). The population status of the northern-wintering group of knots is being assessed, but early evidence (Harrington et al. in prep) does not suggest it is declining. If the population decline of the knots that winter in Patagonia is linked to Delaware Bay food resources, and if the same was true for northern-wintering knots, then we would expect to see commensurable declines in numbers of the northern-wintering knots. Ongoing studies suggest an explanation for this ‘disconnect’ is forthcoming.

Earlier work (Harrington et al. 1988) suggests the northern-wintering group of Red Knots were proportionately less common on Delaware Bay than the Patagonian-wintering group. Recent (2003–2004) feather isotope analyses (Atkinson et al. 2005) suggest that a third of the knots using Delaware Bay during northward migration are from the “northern” wintering area. This suggests that a significant proportion of the northern-wintering knot population migrates through Delaware Bay in spring, and/or that the “northern” group has a substantially larger population size than we have estimated.

ACKNOWLEDGMENTS

We have been helped by many volunteer field assistants, too many to name individually. We especially

thank Patrick and Doris Leary for their extraordinary contributions of information. Our work has benefited substantially from the banding and color-marking programs of other researchers, especially A. K. Baker (Royal Ontario Museum), P. M. Gonzalez (Fundación Inalafquen), L. J. Niles (New Jersey Division of Fish and Wildlife), and K. Kalasz (Delaware Division of Fish and Wildlife). We are grateful to the Georgia Department of Natural Resources and the Manomet Center for Conservation Sciences for support, and to naturalists and other staff of The Lodge at Little Saint Simons Island for field assistance and permission to work on the Island. We thank U.S. Fish and Wildlife Service staff who arranged for Special Use Permits for refuge lands in the Altamaha River Estuary. For helpful suggestions for improvement of earlier drafts of this paper we thank R. I. G. Morrison, T. Piersma, an anonymous reviewer, J. A. Sedgwick, and C. E. Braun.

LITERATURE CITED

- ASHMOLE, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General biology. *Ibis* 103(B):235–273.
- ATKINSON, P. W., A. J. BAKER, R. M. BEVAN, N. A. CLARK, K. B. COLE, P. M. GONZÁLEZ, J. NEWTON, L. J. NILES, AND R. A. ROBINSON. 2005. Unraveling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. *Ibis* 147:738–749.
- BAKER, A. J., R. E. MANRIQUEZ, L. G. BENEGAS, D. E. BLANCO, O. BOROWIK, E. FERRANDO, P. DE GOEIJ, P. M. GONZÁLEZ, J. GONZÁLEZ, C. D. T. MINTON, M. PECK, T. PIERSMA, AND M. S. RAMÍREZ. 1996. Red Knots *Calidris canutus rufa* at their farthest south: an international expedition to Tierra del Fuego, Argentina, in February 1995. *Wader Study Group Bulletin* 79:103–108.
- BUEHLER, D. M. AND A. J. BAKER. 2005. Population divergence times and historical demography in Red Knots and Dunlins. *Condor* 107:497–513.
- BURNS, J. G. AND R. C. YDENBERG. 2002. The effects of wing-loading and gender on the escape flights of Least Sandpipers (*Calidris minutilla*) and Western Sandpipers (*Calidris mauri*). *Behavioural Ecology and Sociobiology* 52:128–136.
- DUGAN, P. J., P. R. EVANS, L. R. GOODYEAR, AND N. C. DAVIDSON. 1981. Winter fat reserves in shorebirds: disturbance of regulated levels by severe winter conditions. *Ibis* 123:359–363.
- GINN, H. B. AND D. S. MELVILLE. 1983. Molt in birds. *British Trust for Ornithology Guide* 19. British Trust for Ornithology, Tring, United Kingdom.
- GUDMUNDSSON, G. A., A. LINDSTRÖM, AND T. ALERSTAM. 1991. Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, Sanderlings *Calidris alba* and turnstones *Arenaria interpres*. *Ibis* 133:140–152.
- HARRINGTON, B. A. 2001. Red Knot (*Calidris canutus*). *The birds of North America*. Number 563.
- HARRINGTON, B. A., J. M. HAGAN, AND L. E. LEDDY.

1988. Site fidelity and survival differences between two groups of New World Red Knots (*Calidris canutus*). *Auk* 105:439–445.
- HAYMAN, P., J. MARCHANT, AND T. PRATER. 1986. Shorebirds: an identification guide to the waders of the world. Houghton Mifflin, Boston, Massachusetts, USA.
- HOLMGREN, N., H. ELLEGREN, AND J. PETTERSSON. 1993. Stopover length, body mass and fuel deposition rate in autumn migrating adult Dunlins *Calidris alpina*—evaluating the effects of moulting status and age. *Ardea* 81:9–20.
- LINDSTRÖM, Å., S. DAAN, AND G. H. VISSER. 1994. The conflict between moult and migratory fat deposition: a photoperiodic experiment with Bluethroats. *Animal Behaviour* 48:1173–1181.
- MORRISON, R. I. G. AND B. A. HARRINGTON. 1992. The migration system of the Red Knot *Calidris canutus rufa* in the New World. *Wader Study Group Bulletin* 64 (Supplement):71–84.
- MORRISON, R. I. G., R. K. ROSS, AND L. J. NILES. 2004. Declines in wintering populations of Red Knots in southern South America. *Condor* 106:60–70.
- SPAANS, A. L. 1978. Status and numerical fluctuations of some North American waders along the Surinam coast. *Wilson Bulletin* 90:60–83.